Phylogenetic incongruence and homoplasy in the appendages and bodies of arthropods: Why broad character sampling is best

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Abstract

Notwithstanding the rapidly increasing sampling density of molecular sequence data, morphological characters still make an important contribution to our understanding of the evolutionary relationships of arthropod groups. In many clades, characters relating to the number and morphological specialisation of appendages are ascribed particular phylogenetic significance, and may be preferentially sampled. However, previous studies have shown that partitions of morphological character matrices often imply significantly different phylogenies. Here, we ask whether a similar incongruence is observed in the appendage and non-appendage characters of arthropods. We apply tree length (incongruence length difference: ILD) and tree distance (incongruence relationship difference: IRD) tests to these partitions in an empirical sample of 52 published neontological data sets for arthropods. We find significant incongruence about one time in five: more often than expected, but markedly less often than in previous partition studies. We also find similar levels of homoplasy within limb and non-limb characters, both in terms of internal consistency and consistency relative to molecular trees. Taken together, these findings imply that sampled limb and non-limb characters are of similar phylogenetic utility and quality, and that a total evidence approach to their analysis is preferable.

Introduction

Despite the increasing ease and economy of obtaining ever larger volumes of molecular phylogenetic data – coupled with progressively more sophisticated models for their analysis – morphological characters can still contribute significantly to resolving the phylogeny of many clades (Wiens, 2004; O'Leary & Gatesy, 2008; Gainett et al., 2014; also see discussion in Lopardo & Hormiga, 2015). Morphological and molecular data are often reciprocally illuminating (e.g. Houde, 1994; Nicolalde-Morejón et al., 2009), and can reveal hidden support when combined in a single total evidence analysis (Kluge, 1989; Gatesy et al., 1999; Gatesy & Arctander, 2000; Wahlberg et al., 2005; Damgaard, 2008; O'Leary & Gatesy, 2008; Padial et al., 2010; Mounce et al., 2016). For fossil species, morphology is typically the only source of phylogenetic data, despite impressive strides in obtaining sub-fossil DNA (e.g. Dabney et al., 2013; reviewed in Shapiro & Hofreiter, 2014; Orlando et al., 2015) and the value of stratigraphic time series in a few special cases (Wills et al., 2008; Wills *et al.* 2009; O'Connor & Wills, 2016). Unlike molecular sequence data, there are no widely implemented standard frameworks for coding and archiving morphological data (but see O'Leary & Kaufman, 2011; Davies *et al.*, 2017). Partly as a result of this, there is little systematic knowledge concerning rates of evolution and levels of homoplasy in morphological characters from different anatomical regions in different clades. Similarly, there is no consensus on the types of morphological characters that are likely to be informative for cladogeneses of different geological ages. Despite this, trees are often inferred from relatively restricted morphological character sets (Sanchez-Villagra & Williams, 1998; Arratia, 2009; Song & Bucheli, 2010; Mounce et al., 2016) (a practice that may be analogous to early molecular phylogenies that used small numbers of loci that may not always have evolved at appropriate rates; Bateman, 1999). For fossil taxa, this may reflect various preservation biases (Sansom et al., 2010, 2017; Sansom & Wills, 2013; Pattinson et al., 2014). For example, molluscs typically lack all soft-part data (Castelin et al., 2017), while ostracods are almost exclusively known from their sculpted, bivalved carapaces (Briggs *et al.*, 1993; Whatley *et al.*, 1993).

Character sampling in arthropods

Biased character sampling may be a particular problem in arthropods, where there is growing evidence that overall levels of homoplasy are greater than in many other higher taxa (Engel, 2015). Examples include the genital morphology of acarine mites (Klimov *et al.*, 2017) and insects (Bennik et al., 2016; Yoshizawa et al., 2016), the wing morphology of lepidopterans (Finkbeiner *et al.*, 2017), the limbs of amphipod crustaceans (Verheye et al., 2016), and the overall morphology of cave-dwelling Diplopoda (Liu *et al.*, 2017) and Collembola (Christiansen, 1960). Moreover, historically, even the deep phylogeny of arthropods has been addressed with restricted character sets, and with a striking diversity of results (e.g. Wheeler *et al.*, 1993; Giribet et al., 2001; Boore et al., 2005; Regier et al., 2005).

Characters pertaining to the number and morphological adaptations of limbs are particularly important for arthropod systematics and phylogenetics (Størmer, 1939; Schulz, 2007; Gainett *et al.*, 2014). Unfortunately, such characters are often poorly recorded in fossil arthropods, and several major groups – notably trilobites (Størmer, 1939; Hughes, 2003) and ostracods (Smith, 2000) – preserve limbs only under the most exceptional circumstances. Here, we address two questions in a sample of 38 arthropod data matrices comprising predominantly extant taxa, and coding a broad sample of characters from both the limbs/mouthparts/antennae (appendages) and the rest of the body. Firstly we ask whether levels of homoplasy differ between appendages on one hand, and body and carapace characters on the other, such that the quality of data in either partition might be deemed superior (see Pettigrew, 1991; Sanchez-Villagra & Williams, 1998; Williams, 2007; Song & bucheli, 2010; Parker, 2016). Secondly we ask whether the hierarchical signals conveyed by appendage and body characters imply different phylogenies (see Mounce *et al.* 2016; Sansom & Wills 2017; Sansom *et al.* 2017).

Why examine morphological character partitions in arthropods?

The rationale for this partitioning is twofold. Firstly, suites of characters can evolve in functionally or developmentally integrated modules (Clarke & Middleton, 2008; Klingenberg, 2008; Lü *et al.*, 2010). These can be subject to different selection pressures and evolve at different speeds (Maynard Smith, 1993; Lü et al., 2010; Parker, 2016), thereby exhausting their character spaces at different rates

(Wagner, 1995,1997; Oyston et al., 2015; Oyston et al., 2016) and containing different levels of homoplasy as a result. For example, Sánchez-Villagra & Williams (1998) demonstrated that strong functional selection for feeding and locomotion increases the evolutionary lability of dental and postcranial characters relative to cranial characters in the skeletons of mammals, while Sansom *et al.* (2017) showed that mammalian dental data exhibit relatively poor congruence with independent molecular phylogenies. Similarly, the mouthparts of insects (Angelini & Kaufman, 2005) and other arthropods (Řezáč *et al.*, 2008; Baiocco *et al.*, 2017) are highly labile and are extensively modified in lineage specific ways, reflecting the trophic resources that they exploit. The same is true of other appendages, which are highly conserved in their underlying structure, but which possess a great diversity of form and function across taxa of all ranks (Angelini & Kaufman, 2005). Relatively high levels of homoplasy can also be found in arthropod body characters. For example, the classification of ostracod crustaceans is heavily contingent on characters of the carapace (Tinn & Oakley, 2008), despite marked and misleading convergence in form. Characters of the copulatory limbs, by contrast, are much more conserved and less homoplastic (Park *et al.*, 2000; Cohen & Morin, 2003).

Secondly, much of the arthropod (particularly insect) fossil record is concentrated within a relatively small number of Konservat-Lägerstatten (Sepkoski, 1981; Martinez-Delclòs *et al.*, 2004; Baalbergen & Donovan, 2013). Outside of these exceptional localities, there are usually conspicuous biases in the suites of characters or anatomical regions preserved. For example, Baalbergen & Donovan (2013) found only the chelae of decapod crustaceans preserved (despite unusually good preservation of other arthropod groups at the same site), while Stempien (2005) reported that the chelipeds and carapaces of Brachyura were more likely to fossilize than their walking legs. Similarly, tough, sclerotized structures such as the elytrae (Martinez-Delclòs *et al.*, 2004; Baalbergen & Donovan, 2013) of insects are more frequently preserved than many other body parts. The calcite carapaces of ostracods frequently preserve highly homoplastic and functionally constrained details of sculpture and ornamentation, whereas limbs are only rarely fossilised (Smith, 2000). Among fossil Arachnomorpha, the taxonomically diagnostic chelicerae are rarely reserved, obfuscating the systematic placement of many specimens (Dunlop, 1997). Hence, body characters such as differentiation of the opisthosoma and segmentation of the post-abdomen are more useful in fossil chelicerate systematics (Dunlop,

1997). Such anatomical biases on character sampling could mislead attempts to infer the relationships of fossil arthropods, particularly if homoplasy is concentrated within the more readily preserved characters.

Materials & Methods

Datasets

The character matrices utilised in this study were obtained from peer-reviewed papers published between 2000 and 2017. We sought to sample all major living arthropod groups (Chelicerata, Pancrustacea (Crustacea and Hexapoda), Myriapoda), including matrices of varying dimensions and clades of both lower and higher ranks (genera through classes). Wherever possible, more recent and more inclusive matrices were used. We utilised Graeme Lloyd's online compilation of matrices (Lloyd,) and searches of Web of Science using higher taxon names plus the root keywords "phylog* + morphol*". The resulting sample of 52 matrices contained representatives of 21 orders in 7 classes (see Tables 1, 2). 38 matrices were collected for the incongruence tests and internal consistency tests and 15 crustacean matrices were collected for the molecular consistency tests (see below).

Definition of character partitions

The "appendage" character partition included those pertaining to the legs and leg-derived appendages. This encompassed all podomeres of the walking legs and modified legs such as brooding limbs (e.g., Jenner *et al.*, 2009) and the spinnerets of spiders (Selden *et al.*, 2008). Also included were characters pertaining to the mouthparts, including mandibles, maxillae, and the labium (Angelini & Kaufman, 2005), as well as the palps, chelicerae and glossae. The labrum, hypopharynx and epipharynx were also included in the "appendage" partition as they are closely functionally associated with the other mouthparts and in some groups form a feeding apparatus for sucking or piercing in conjunction with these other elements (Angelini & Kaufman, 2005). As such, we suspect that they are subject to similar selective pressures (Klingenberg, 2008). Antennae were also included (Angelini & Kaufman, 2005), as were genital structures derived from legs or fused coxae such as the hypandria. Characters

pertaining to setation or other elaborations of leg, mouthpart or appendage podomeres were also included, as were characters referring to limb musculature.

The "body" character partition was defined, by default, as all those characters not encompassed above. This included the wings and elytrae of insects, since we consider these to be derived from the carapace of the thorax rather than from pre-existing limb structures (Clark-Hatchel & Tomoyasu, 2016). The "body" partition also included all characters encoding genital structures that were not derived from appendages, such as those pertaining to the vulva, genital pore, spermatheca and ovipositor. Characters pertaining to elaborations and ornamentations of body segments were included with the "body" partition, as where characters of the eyes and internal organs. Behavioural, molecular, developmental and sperm characters were removed from each matrix (these accounted for just 3% of those analysed).

Missing and inapplicable codes

Poorly known taxa (or those that were otherwise scored for only a small number of characters) can be highly mobile in sets of optimal trees; particularly those inferred using maximum parsimony. This can, in turn, result in large numbers of MPTs, prohibitively long search times and poor resolution of consensus trees (Wilkinson, 1995; Mounce et al., 2016). Where data matrices were found to be subject to these issues empirically, we edited them (using Mesquite Version 3.40: Maddison & Maddison 2018) by removing taxa with more than 75% of characters scored as missing ("?") or inapplicable ("-") in either partition (50% for the data set of Schulz, 2007). We also removed taxa found to be taxonomically equivalent to others (*sensu* Wilkinson, 1995). Any characters rendered uninformative or invariant by this process were also deleted. A mean of just 0.47 taxa (~2.2%) and 3.34 characters (~3.6%) were removed from each dataset in this manner (for a list of the precise taxa and characters deleted, see Appendix 1).

We did not set out to analyse matrices of fossils, since our intention was to compare signals in limb and non-limb characters. Fossil taxa often tend to contain larger proportions of missing codings (Wilkinson, 1995; Wiens, 1998; Mounce et al., 2016), and these missing codes tend to be concentrated in characters pertaining to regions of anatomy with lower preservation potential. In

particular, fossils tend to lack data for limbs and other appendages. However, fossils are often informative in phylogenetic analyses of arthropods (Legg et al., 2013) and other taxa (Cobbett *et al.* 2007), so fossil taxa within matrices of predominantly extant taxa (e.g. Schulz, 2007; Olesen, 2009; Liu et al., 2012) were not discounted *a priori*, but only as a consequence of obfuscating analyses as described above.

Measuring homoplasy

We took two approaches to measuring homoplasy: internal consistency of morphological characters relative to the most parsimonious trees derived from those same morphological characters, and molecular consistency of morphological characters when optimised onto independent molecular trees (e.g. Sansom *et al.* 2017, Sansom and Wills 2017). With both approaches, we used the ensemble Consistency Index (CI; Kluge & Farris, 1969) and ensemble Retention Index (RI; Farris, 1989). CI is a commonly used and well-characterised index of homoplasy. However, it is subject to known biases, notably a correlation with the number of characters and taxa in the dataset (Archie, 1989; Mounce *et al.* 2016). For the internal CI, we removed these biases empirically by comparing the residuals from regression analyses of CI on both matrix dimensions. For comparisons of the CI of morphological character partitions optimised into molecular trees, however, there are no such biases because the (molecular) trees are not inferred from the (morphological) data. For molecular consistency tests, we sought independent molecular trees (Sansom and Wills 2017, Sansom *et al.* 2017). Taxa were pruned (typically from the morphological data set) such that both morphological and molecular trees had the same residual leaf set. This had the potential to render some morphological characters uninformative, and these were subsequently removed from the matrix. Internal consistency measures were derived using *PAUP* 4.0a.154* (Swofford, 2017) whilst molecular consistency measures were derived using *TNT* (Goloboff, 2008) and *Mesquite* (Maddison & Maddison, 2018).

Statistical tests for incongruence

The Incongruence Length Difference (ILD) test (Mikevich & Farris, 1981; Farris *et al.*, 1995a; Farris *et al.*, 1995b) is a widely implemented partition homogeneity test based upon the difference in most

parsimonious tree (MPT) length for a matrix when analysed as a whole, and the sum of MPT lengths for the partitions of the matrix analysed in isolation (MPTs). More formally, the ILD for a bi-partitioned matrix is given by $L_{AB} - (L_A + L_B)/L_{AB}$, where L_{AB} is the optimal tree length (in steps) from the analysis of the entire matrix (the total evidence analysis), and L_A and L_B are the optimal tree lengths for partitions A and B analyzed independently. This ILD is compared with a distribution of ILD values (here, 999) for random bipartitions of the matrix in the same proportions as the original, and a p value is derived from the fraction of these as large or larger than the original. The ILD test has been criticized on philosophical grounds, and because it has a high Type I error rate (Dolphin *et al.*, 2000; Barker & Lutzoni, 2002; Ramirez, 2006; Sansom *et al.* 2017). However, it remains very widely applied (Mounce *et al.*, 2016), and is used here as a measure of matrix partition incongruence rather than as a criterion for combining those partitions (Figure 1).

In addition to the ILD test, we also implemented the incongruence relationship difference (IRD) test of Ruta & Wills (2016) and Mounce *et al.* (2016). This is analogous to the ILD test in that a measure of incongruence for the original data partition is compared with a distribution of incongruence values for a large number of random partitions. However, whereas for the ILD incongruence is measured in terms of additional tree length, a tree-to-tree distance metric is used for the IRD. Many such metrics are available, but here we use two tests based upon the symmetrical-difference (RF) distance (IRD_{RF}; Robinson & Foulds, 1981) and maximum agreement subtree (MAST) distance (IRD_{D1}; Goddard et al., 1994; de Vienne et al., 2007). We acknowledge that other metrics may have more desirable properties, but the RF distance in particular well characterised and widely applied. It is unusual for a single most parsimonious tree (MPT) to result from a parsimony search, and we therefore followed Mounce *et al.* (2016) in calculating the mean nearest neighbour distance (NND) between each tree resulting from one partition and the most similar tree in the other partition. In addition, we calculated the distances between strict, semi-strict and 50% majority rule (plus compatible groupings) trees for the two partitions, although we caution that these offer poor or positively misleading summaries of the differences between sets of trees (Mounce *et al.* 2016). We illustrate this latter approach for the eumalacostracan data of Jenner *et al.* (2009) and Wills *et al.* (2009) (Figure 2), and for the myriapod data of Blanke and Wesener (2014) (Figure 3). IRD tests were

initially based upon 99 random partitions of the data (c.f .999 for the computationally much faster ILD). However, in those cases where $p \leq 0.10$, we re-ran the test for that data set using 499 random partitions (Figure 1).

All parsimony searches were implemented using 25 random additions of taxa, followed by tree bisection and reconnection branch swapping, and retaining 10 trees at each step. To expedite the searches, we limited the number of trees stored in memory to 100,000, and for the IRD tests we calculated nearest neighbour tree-to-tree distances based upon no more than 1,000 trees from each partition (2,000 trees in total and 1,999,000 tree-to-tree distances calculated for each metric in order to find the minima). Consensus trees were calculated from all MPTs, up to the 100,000 buffer. We also condensed the resulting most parsimonious trees by collapsing branches with a minimum length of zero (Goloboff's 'amb-') and removing all but one of any consequently identical trees. All analyses were implemented in PAUP* 4.0a.154 for Macintosh (Swofford, 2017), using scripts (by MAW) that produced batch files for PAUP* and summarised the log files that it produced (see Supplementary Materials).

Results

There is no difference in levels of homoplasy (CI) or retained synapomoprhy (RI) for limb and body characters

There were no significant differences in mean levels of internal homoplasy (as measured by the ensemble Consistency Index, CI) between limb and body partitions, either for the 38 datasets in combination, or for subphyla considered in isolation ($p > 0.05$ in all cases) (Fig. 5). To account for the known biases in CI, residuals from regression analyses of internal CI on both the log of the number of characters and the log of the number of taxa were also compared across partitions. The results differed little from those for raw CI (Figure 4), and no significant differences were detected. A similar set of analyses for retained synapomorphy (as measured by the Retention Index: RI) also revealed no differences between limb and body partitions, either overall or within subphyla. Our findings were similar for the 15 crustacean data sets for which we had independent molecular trees: there were no

differences between the CI or the RI of limb versus body character partitions when optimised onto those molecular trees ($p<0.05$ for paired t tests) (Fig. 5).

Limb and body partitions imply significantly different trees one time in five

Both the ILD test and the IRD_{RF} test for nearest neighbours reported significant ($p<0.05$) incongruence between the trees inferred from limb and body character partitions in about one in five cases (8/38 and 7/38 respectively). The IRD_{D1} test for nearest neighbours reported significant ($p<0.05$) incongruence slightly less often (5/38). We note that the different tests assess different aspects of incongruence, and the p values for ILD, IRD_{RF} and IRD_{D1} do not precisely coincide. Hence, a significant p-value ($p<0.05$) is obtained for both IRD_{RF} and IRD_{D1} in 3 datasets, and for all three tests (including the ILD) in only 2 cases. Rates of significant incongruence are summarised in Table 2. For the ILD test, our finding that 8 from 38 data sets were incongruent with $p\leq0.05$ means that incongruence is significantly more common than expected by chance (two would be anticipated: binomial test $p=0.0005$). The IRD_{RF} test also detected significant incongruence significantly more often than expected ($p = 0.0025$). Whilst reporting significant incongruence at the lowest rate, the IRD_{D1} test also detected a significantly higher rate of incongruence than would be expected ($p = 0.03973$, binomial test).

The outcome of the ILD and IRD tests is not significantly influenced by data set parameters or by taxonomic group

We sought to determine whether various data set dimensions and imbalances might determine the outcome of our incongruence tests ($p\leq 0.05$ or $p>0.05$). In addition to data matrix dimensions, previous studies (e.g., Mounce et al., 2016; Sansom *et al.* 2013, 2017.) have accounted for (or variously controlled) amounts of missing data within partitions or regions. In general, we found that there was no significant difference in the median percentage of cells scored as missing/inapplicable for limb and body partitions across the entire data set (Mann-Whitney $U = 36.9636$, $p = 0.4242$). Neither were there significant differences in the mean or variances of percentages of missing/inapplicable codings for limb and body partitions within individual sub-phyla: myriapods

(paired t = -0.3868, p = 0.7148), crustaceans (paired t = -0.5852, p = 0.5768), chelicerates (paired t = -0.7982, p = 0.4510), hexapods (paired t = -0.4896, p = 0.6315) (Fig. 6). For each data set, however, we also took account of the difference in percentage of missing data between partitions (this was a marginally significant factor in the study of Mounce *et al.*, 2016). However, a logistic regression model (see Appendix 2) showed that the outcome of the ILD was not significantly influenced by the log of the percentage of missing data across both partitions (p=0.6127), the difference in the percentage of missing data between partitions (p=0.1551), the difference between partition sizes (p=0.1564), the log of the number of taxa (p=0.0606), log of the number of characters (p=0.0667) or the interaction between these last two variables (p=0.0619). The model also showed that higher taxonomic group (i.e., Chelicerata, Crustacea, Hexapoda, Myriapoda) had no effect on ILD outcome. Similarly, a log-likelihood ratio test (G-test) revealed no difference in the frequencies of significant or non-significant outcomes across these higher taxa (G = 4.0863, p = 0.2523). We found similar results from logistic modelling of the outcome of the IRD_{RF} and IRD_{D1} tests, with no significant effect for overall percentage of missing data (p=0.511 and p=0.396), the difference in percentage of missing data between partitions (p=0.330 and p=0.987), the log of the number of taxa (p=0.838 and p=0.379), log of the number of characters (p=0.692 and p=0.417), or the interaction between characters and taxa (p=0.727 and p=0.381). Higher taxonomic group also had no effect for either test, and G-tests also revealed no difference in the frequency of significant outcomes for the four groups (IRD_{RF}, G = 2.7948, p = 0.4244: IRD_{D1}, G = 1.4049, p = 0.7044).

Limb and body character sampling

Overall there was no significant difference in the log of number of characters sampled from each partition of the datasets in Table 1 (t = -0.3461, p = 0.7312, paired t-test of logs). Furthermore, no significant difference was observed in chelicerates (t = -0.5679, p = 0.5907, paired t-test) or myriapods (t = 2.1830, p = 0.0808, paired t-test). However, differences were observed within crustaceans (t = 2.7658, p = 0.0279, paired t-test of logs) and hexapods (t = -4.4382, p = 0.0005, paired t-test of logs). Crustacean datasets contained significantly more limb characters than those from the body, while the opposite tendency pertained in hexapod datasets. We do not assume that

these differences reflect a bias of sampling from the hypothetical universe of possible leg and body characters, since there is no reason to suppose that the two partitions should yield identical character numbers (a naïve null hypothesis). Rather, we merely report that the numbers do, in fact, differ in the case of crustaceans and hexapods.

Discussion and Conclusions

1. Levels of incongruence

Rates of significant ($p<0.05$) incongruence between limb and body partitions across our sample of arthropod matrices were significantly higher than expected for all of our tests. We found 8 from 38 significant with $p\leq0.05$ for the ILD (one in five) and 7 from 38 for the IRD_{RF}, whereas two (one in twenty) would be expected by chance (binomial test $p=0.0005$). The only previous, systematic studies of partition homogeneity using similar approaches to those deployed here concerned the craniodental and postcranial characters of vertebrates (Mounce *et al.*, 2016), the dental and osteological characters of mammals (Sansom *et al.*, 2017) and hard and soft part characters across a diversity of animal clades (Sansom & Wills, 2017). Higher rates of significant ($p<0.05$) incongruence were reported in those earlier studies: about 1 in 3 (ILD and IRD) for craniodental/body characters and hard/soft characters, and up to 1 in 2 (ILD) for dental/osteological characters (compared with 1 in 5 for the ILD and IRD across our arthropods). There is no reason to expect limb versus body partitions for arthropods to yield similar rates of null rejection to functionally and anatomically different partitions in other groups. However, levels of limb to body incongruence for our sample of arthropods are not especially high, and this is good news for those attempting to infer the relationships of fossil arthropods that lack details of appendage morphology, provided there is enough character data overall.

Lack of partition homogeneity can result from a variety of factors other than conflict between the phylogenetic signals inherent in partitions (Mounce *et al.*, 2016; Dolphin *et al.*, 2000; Planet, 2006). However, we demonstrate that there are no significant ($p < 0.05$) differences in overall levels of either internal or molecular consistency between the partitions of our data sets (CI and RI, Figures

4, 5), and neither are there differences in amounts of missing data. Although the levels of homoplasy contained within each partition may be comparable, the quality of this noise often misinforms the inference of phylogenies in different ways, thereby resulting in incongruence.

2. Implications of incongruence

Whatever the cause of the incongruence between partitions, it is still observed more often than we would expect, with several implications. Focussing on restricted suites of characters to the exclusion of others is questionable practice, unless it has been demonstrated *a priori* (e.g., in a large empirical sample: Sansom *et al.*, 2017; Sansom and Wills, 2017) that some classes of characters are intrinsically more informative and less prone to homoplasy than others. This is not the case for the appendage and body characters of arthropods. Nevertheless, uneven character sampling is commonplace in arthropod systematics (Clarke, 2011), and we find these biases in some higher taxa here. Such biases probably reflect previous expectations that certain characters are of more value or contain a stronger phylogenetic signal than others (see Sanchez-Villagra & Williams, 1998; Williams, 2007; Song & Bucheli, 2010; Parker, 2016; Mounce *et al.*, 2016; Sansom *et al.*, 2017). For example, Gainett *et al.* (2014) focused upon appendicular characters in their phylogeny of harvestmen, while Dunlop (1997) found that characters of body segmentation and segment differentiation were particularly helpful in determining the higher-level relationships of chelicerates (Dunlop, 1997). Our sample of data sets does not support this idea for limb and body characters across arthropods.

Such biases are most acute (and often unavoidable) in many fossil groups, where the more heavily mineralized or sclerotized cuticle of the carapace and tergites typically preserve more readily than that of the limbs. Hence, many fossil arthropod taxa lack details of the appendages, and focus, out of necessity, on 'body' characters of segmentation and ornamentation. In ostracods, for example, body characters are the most readily available (Tinn & Oakley, 2008), despite suggestions that appendicular characters are of much greater utility (Park *et al*., 2002; Cohen & Moren, 2003). Notwithstanding, many arthropod studies uncover hidden support and hidden branch support (Gatesy et al., 1999) from combined suites of morphological characters (Clarke, 2011) and from the combination of morphological and molecular data (e.g. Damgaard, 2008; Wahlberg *et al.*, 2005). We

385 therefore advocate holistic character sampling (Song & Bucheli, 2010) and principles of total
386 evidence (Kluge, 1989; Gatesy & Springer, 2014; Mounce *et al.*, 2016; see also Gatesy & Arctander,
387 2000) in arthropod phylogenetics.

388 There are other systematic problems that may occur when trees are inferred from non-random
389 character samples, although these are usually framed in terms of the effects of missing data. In this
390 regard, it is not the number of missing entries in a matrix so much as the amount of data that *are*
391 present that influences the resolution of trees and the stability of taxa within them (Wiens, 2003ab;
392 Cobbett *et al.*, 2007). Non-random blocks of missing data – such as those that typically result from
393 the concatenation of molecular data sets with different taxon samples (Chernomor *et al.*, 2016;
394 Dillman *et al.*, 2016; Dobrin *et al.*, 2018) or morphological data sets containing a mix of fossil and
395 extant taxa (Pattinson *et al.*, 2015; Sansom, 2015) – bring their own particular set of problems. The
396 processes of decay prior to fossilisation obliterate soft part character data, but a recent and surprising
397 finding is that such characters tend to optimize along branches further from the root of the tree than
398 their more fossilizable counterparts. The simulated removal of soft part data from species within real
399 neontological data sets therefore tends to result in the disproportionate 'stemward slippage' of
400 lineages towards the root of the tree (Sansom & Wills, 2013; Sansom, 2015). It is therefore likely that
401 many fossils appear more plesiomorphic and erroneously resolve closer to the roots of phylogenies as
402 a function of taphonomic filters (Sansom *et al.*, 2017). This needs to be explored on greater detail
403 across the phylogeny of arthropods.
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Author, Year	Clade	Taxa	Limb chrs	Body chrs	% missing limb	% missing body	IRD_{RF}	IRD_{D1}	ILD	CI limb	CI body	RI limb	RI body
	Chelicerata												
Bochkov et al., 2010	Acari: Psoroptidae: Makialginae	11	27	23	1.01	5.93	0.084	0.142	0.751	0.70	0.79	0.77	0.81
Botero-Trujillo et al., 2017	Solifugae: Mummuciidae	15	14	6	2.38	9.33	0.072	0.152	1.000	1.00	0.90	1.00	0.75
Klompen et al., 2013	Acari: Heterozerconidae	10	23	6	3.04	1.67	0.56	0.81	0.202	0.60	0.75	0.58	0.80
Kuntner, 2005	Araneae: Nephilidae: Nephilinae	28	69	88	13.35	13.46	0.182	0.019	0.002	0.52	0.42	0.72	0.73
Mendes, 2011	Opiliones: Laniatores: Gonyleptidae	21	46	56	11.49	13.10	0.029	0.499	0.061	0.56	0.44	0.71	0.63
Prendini & Esposito, 2010	Scorpiones: Buthidae	29	28	38	0.37	1.72	0.182	0.020	0.097	0.55	0.48	0.81	0.77
Schulz, 2007	Arachnida	44	77	86	7.76	10.31	0.72	0.86	0.014	0.61	0.56	0.88	0.84
Wood et al., 2012	Araneae: Archaeidae	37	75	51	28.43	21.67	0.75	0.56	0.010	0.48	0.48	0.78	0.79
	Crustacea												
George, 2017	Copepoda: Laophontodinae	9	32	18	4.17	0.62	0.022	0.019	0.033	0.49	0.44	0.64	0.66
Jenner et al., 2009	Eumalacostraca	24	99	63	9.60	19.44	0.016	0.159	0.008	0.49	0.44	0.64	0.66
McLaughlin et al., 2007	Anomura: Paguroidea	20	34	45	1.18	0.22	0.229	0.387	0.507	0.56	0.47	0.66	0.59
Olesen, 2009	Branchiopoda	15	44	28	30.45	29.76	0.631	0.459	0.122	0.84	0.85	0.75	0.84
Richter & Scholz, 2001	Malacostraca	19	34	41	10.22	22.21	0.098	0.461	0.161	0.59	0.58	0.68	0.65
Riehl et al., 2014	Isopoda: Asellota: Urstylidae	28	283	124	15.57	26.64	0.294	0.950	0.002	0.52	0.56	0.76	0.70

Vereshchaka et al., 2016	Decapoda: Luciferidae	29	119	48	33.20	24.31	0.390	0.330	0.213	0.72	0.74	0.85	0.91
Vereshchaka & Lunina, 2015	Decapoda: Sergestidae	23	100	48	24.40	19.02	0.51	0.22	0.223	0.72	0.78	0.72	0.83
	Hexapoda												
Banks & Paterson, 2004	Phthiraptera: Philopteridae	16	14	41	1.79	7.47	0.59	0.29	0.624	0.85	0.58	0.94	0.74
Blagoderov *et al.*, 2009	Diptera: Sciaroidea: Lygistorrhinidae	18	25	35	10.47	7.14	0.81	0.920	0.121	0.55	0.45	0.67	0.60
Calor & Holzenthal, 2008	Trichoptera: Leptoceridae	11	10	21	9.09	12.99	0.099	0.269	0.411	0.86	0.74	0.93	0.82
Chamorro & Konstantinov, 2011	Coleoptera: Chrysomelidae: Lamprosomatinae	13	5	21	12.30	3.66	0.042	0.011	0.103	1.00	0.81	1.00	0.85
Clarke, 2011	Coleoptera: Staphylinidae	24	26	104	2.16	1.64	0.32	0.190	0.616	0.68	0.55	0.86	0.77
Del Rio *et al.*, 2012	Coleoptera: Curculionidae: Entiminae	11	9	40	0.00	5.23	0.45	0.35	0.691	0.68	0.58	0.58	0.55
Di Guilio *et al.*, 2003	Coleoptera: Carabidae	9	26	30	0.85	16.30	0.46	0.57	0.703	0.76	0.75	0.76	0.77
Gerstmeier & Eberle, 2011	Coleoptera: Cleridae: Clerinae	12	10	13	2.50	8.33	0.180	0.820	0.062	0.61	0.50	0.72	0.68
Grebennikov & Newton, 2009	Coleoptera: Scydmaenidae	38	106	105	3.80	5.66	0.57	0.51	0.042	0.34	0.30	0.70	0.66
Grebennikov, 2010	Coleoptera: Curculionoidea	16	10	13	6.25	7.21	0.220	0.210	0.014	0.84	0.96	0.82	0.94
Liu *et al.*, 2012	Megaloptera: Chauliodinae	24	17	24	18.38	6.08	0.450	0.044	0.921	0.85	0.54	0.95	0.81
Michel-Salzat	Hymenoptera:	23	19	18	4.58	0.00	0.089	0.056	0.191	0.79	0.76	0.95	0.95

***et al.*, 2004**	Apinae: Euglossini												
Packer et al., 2017	Hymenoptera: Megachilidae	27	87	127	1.53	6.27	0.23	0.79	0.362	0.41	0.36	0.68	0.65
Wipfler *et al.*, 2010	Grylloblattodea	18	49	55	6.24	8.83	0.33	0.61	0.924	0.64	0.67	0.67	0.72
Yoshizawa, 2004	Psocoptera: Psocidae	14	11	22	7.79	2.92	0.27	0.26	0.390	0.75	0.81	0.84	0.90
Yoshizawa & Leinhard, 2010	Psocoptera: Liposcelididae	14	9	16	0.00	8.93	0.32	0.32	0.845	0.71	0.93	0.81	0.83
	Myriapoda												
Blanke & Wesener, 2014	Diplopoda	16	23	33	2.99	5.11	0.015	0.027	0.094	0.87	0.74	0.94	0.86
Edgecombe & Barrow, 2007	Chilopoda: Scutigeromorpha	21	41	14	10.57	17.35	0.53	0.99	0.407	0.91	0.79	0.97	0.92
Koch et al., 2009	Chilopoda: Scolopendromorpha	30	46	34	2.54	19.31	0.030	0.520	0.089	0.60	0.60	0.85	0.86
Pena-Barbosa et al., 2009	Diplopoda: Polydesmida: Chelodesmidae	15	31	16	17.20	8.33	0.457	0.904	0.689	0.61	0.62	0.76	0.80
Pitz & Sierwald, 2010	Diplopoda: Helminthomorpha	33	34	20	7.75	0.00	0.98	0.24	0.800	0.46	0.63	0.74	0.78
Wesener & Vanden-Spiegel, 2009	Diplopoda: Sphaerotheriida	38	48	41	1.15	1.16	0.110	0.240	0.053	0.55	0.60	0.83	0.83

780

781 **Table 1** – Summary of the 38 published morphological datasets across all arthropod groups utilised in this study, and the results of all tests. IRD test results

782 based upon 999 randomisations (where quoted to 3 decimal places) or 99 randomisations (where quoted to 2 decimal places, and were $p < 0.20$).

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Morphology Author, Year	Molecular Author, Year	Clade	Taxa	Limb chrs	Body chrs	CI limb	CI body	RI limb	RI body
		Crustacea							
Admowicz & Purvis 2006	Meland & Willassen 2004	Pseudomma	18	26	5	0.31	0.28	0.30	0.23
Bradford-Grieve et al., 2010.	Blanco-Bercial et al., 2011	Calanoida	29	93	7	0.29	0.53	0.58	0.75
Bradford-Grieve et al., 2017	Bradford-Grieve et al., 2017	Megacalanidae	12	37	5	0.29	0.53	0.58	0.75
Chang et al. 2016	Chang et al. 2016	Nephropidae	13	23	28	0.62	0.65	0.75	0.75
Dreyer & Wägele 2001	Dreyer & Wägele 2001	Bopyridae	21	37	13	0.50	0.65	0.66	0.73
Hermoso-Salazar et al., 2008	Hultgren et al., 2014	Synalpheus	13	22	12	0.45	0.44	0.40	0.17
Karasawa et al., 2013	Bracken-Grissom et al., 2014	Pleocyemata	19	22	43	0.87	0.51	0.95	0.72
Lörz & Brandt	Lórz & Held 2004	Epimeriidae	16	41	49	0.45	0.46	0.67	0.54
Oakley et al., 2012	Tinn & Oakley 2008	Ostracoda	34	22	12	0.77	0.75	0.92	0.93
Robalino et al., 2016	Ma et al., 2009	Penaeidae	37	103	94	0.34	0.27	0.63	0.54
Schnabel et al., 2011	Schnabel et al., 2011	Anomura	64	58	61	0.32	0.35	0.76	0.76
Tshudy et al., 2007	Chan et al., 2009	Metanephrops	10	8	14	0.47	0.54	0.44	0.64
Wills et al., 2009	Jenner et al., 2009	Eumalacostraca	14	59	54	0.35	0.39	0.23	0.32
Wilson 2009	Wilson 2009	Peracarida	75	124	55	0.29	0.27	0.69	0.68
Wyngaard et al., 2010	Wyngaard et al., 2010	Mesocyclops	15	41	9	0.62	0.40	0.67	0.40

Table 2 – Summary of the 15 published crustacean morphological and molecular datasets used for molecular consistency tests

Figure 1 – Calculation of p values associated with the Incongruence Length Difference (ILD) test (Mikevich & Farris, 1981; Farris *et al.*, 1995a; Farris *et al.*, 1995b) and the Incongruence Relationship Difference (IRD) test (Ruta & Wills 2016; Mounce *et al.*, 2016) using the Robinson Foulds (RF) distance (IRD_{RF}). **A.** A hypothetical data set is partitioned into 'limb' characters (left hand) and 'non-limb' or body characters (right hand). For illustrative purposes, limb and non-limb character numbers are both contiguous, and both partitions are the same size. This need not be the case. Each matrix partition is then analysed independently using PAUP*, and a single most parsimonious tree (MPT) is inferred from each. The lengths of these are summed (marked *). The incongruence length difference (ILD) is not shown here, but would be equivalent to the difference between this summed length and the length of the MPT(s) resulting from the analysis of both partitions simultaneously). The number of nodes unique to one or both trees is also tallied as the Robinson Foulds (RF) distance (†). **B.** Characters are partitioned at random to yield null distributions of sums of lengths and RF distances. Random partitions contain the same number of characters as the original partitions, and the procedure is repeated a large number of times (999 in this example). **C.** The randomised partitions in 'B' yield empirical distributions of sums of tree lengths (left hand histogram, ILD) and RF distances (right hand histogram, IRD_{RF}). The ILD p-value is calculated as the fraction of the random partitions (plus the original partition) for which the sum of MPT tree lengths is less than or equal to that for the original partition (p = 126/1000 = 0.126). Random partitions with sums of lengths less than the original are those in which the internal consistency of each partition ('leg' or 'body') is greater than that in the original. The IRD_{RF} p-value is calculated as the fraction of the random partitions (plus the original partition) for which the sum of MPT tree lengths is greater than or equal to that for the original partition (p = 384/1000 = 0.384).

Figure 2 – Tanglegram of the 50% majority rule consensus (plus compatible groupings) trees inferred from the "limbs" (left) and "body" (right) partitions of the eumalacostracan data of Jenner et al. (2009) and Wills et al. (2009). The IRD_{RF} test revealed the partitions to be significantly incongruent (p=0.016). Nodes unique to each tree are marked with black dots: only two nodes are shared by the trees inferred from the "limb" and "body" partitions. Majority rule trees are figured for illustrative

purposes. We advocate measures based upon the mean distance between nearest neighbours in the two partitions.

Figure 3 – Tanglegram of majority consensus trees implied by a "limbs" (left) and "body" (right) partition of the diplopod data of Blanke & Wesener (2014), shown to be significantly incongruent by IRD_{RF} ($p=0.015$) and IRD_{D1} ($p=0.025$). Unique nodes in each phylogeny are indicated by black dots. In this case, the tree inferred from the "limbs" partition contains all of the same nodes as the strict consensus tree derived from the entire data set by Blanke & Wesener (2014).

Figure 4 – **A.B.** Box and whisker plots of the distribution of ensemble CI (A) and RI (B) values obtained for limb and non-limb partitions of 38 datasets across all arthropod groups (summarised in Table 1). There were no significant differences in CI or RI between partitions overall, or in any individual taxonomic grouping. **C.D.** Boxplots comparing residual CI (C) and RI (D) values for the same sample of datasets, modelling out the effects of data matrix dimensions (number of characters and number of taxa). There were no significant differences between the partitions, either overall or in any individual taxonomic grouping.

Figure 5 – Box and whisker plots of the distribution of ensemble CI and RI (B) values obtained for limb and non-limb partitions of 15 morphological datasets of crustaceans. Characters have been optimised onto corresponding but independently derived molecular trees for the same leaf set (summarised in Table 2). There were no significant differences in CI or RI between partitions.

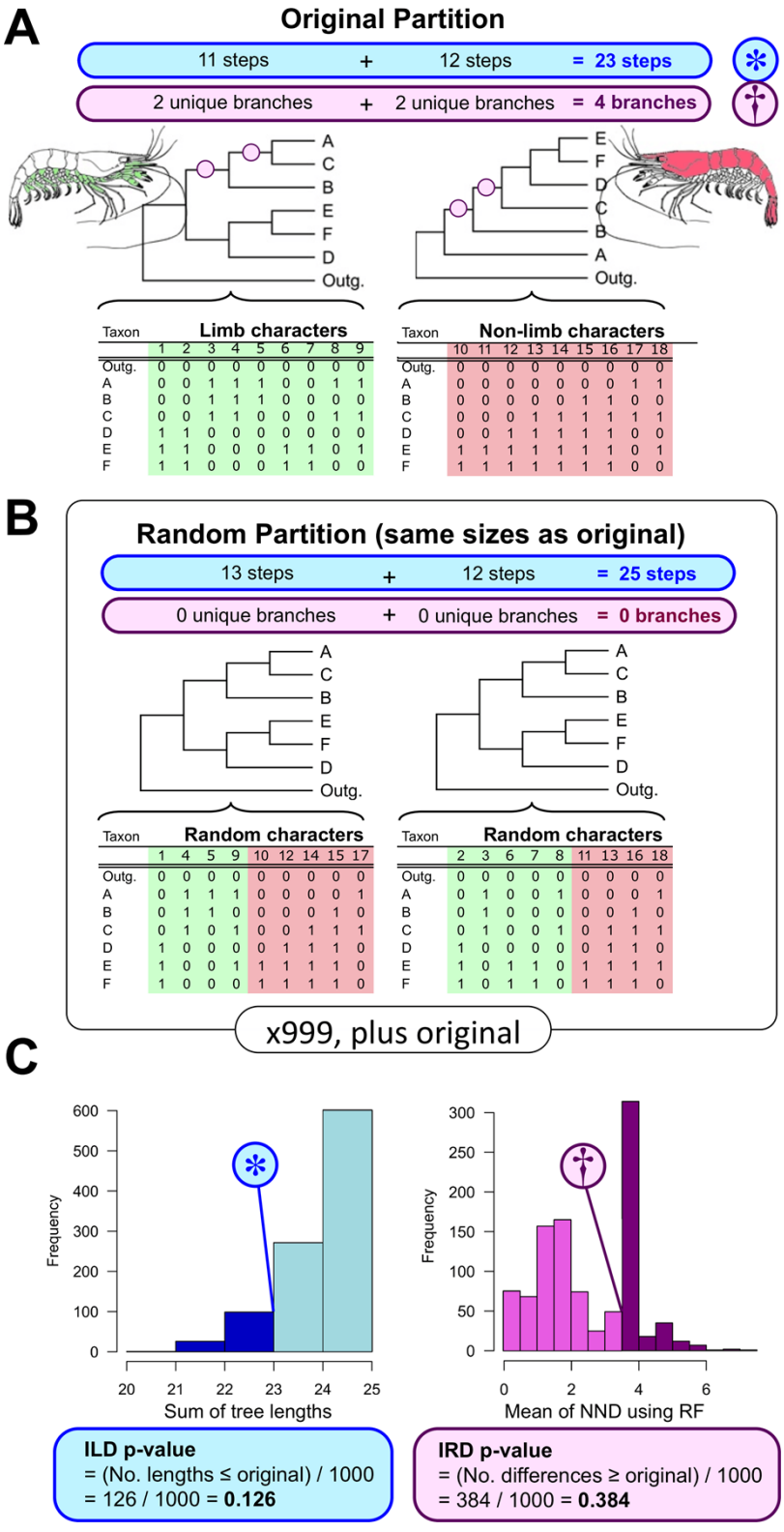

A
Original Partition
11 steps + 12 steps = 23 steps
2 unique branches + 2 unique branches = 4 branches
A C B E F D Outg.
E F D C B A Outg.
Taxon Limb characters
1 2 3 4 5 6 7 8 9
Outg. 0 0 0 0 0 0 0 0 0
A 0 0 1 1 1 0 0 1 1
B 0 0 1 1 1 0 0 0 0
C 0 0 1 1 0 0 0 1 1
D 1 1 0 0 0 0 0 0 0
E 1 1 0 0 0 1 1 0 1
F 1 1 0 0 0 1 1 0 0
Taxon Non-limb characters
10 11 12 13 14 15 16 17 18
Outg. 0 0 0 0 0 0 0 0 0
A 0 0 0 0 0 0 0 1 1
B 0 0 0 0 0 1 1 0 0
C 0 0 0 1 1 1 1 1 1
D 0 0 1 1 1 1 1 0 0
E 1 1 1 1 1 1 1 0 1
F 1 1 1 1 1 1 1 0 0
B
Random Partition (same sizes as original)
13 steps + 12 steps = 25 steps
0 unique branches + 0 unique branches = 0 branches
A C B E F D Outg.
A C B E F D Outg.
Taxon Random characters
1 4 5 9 10 12 14 15 17
Outg. 0 0 0 0 0 0 0 0 0
A 0 1 1 1 0 0 0 0 1
B 0 1 1 0 0 0 0 1 0
C 0 1 0 1 0 0 1 1 1
D 1 0 0 0 0 1 1 1 0
E 1 0 0 1 1 1 1 1 0
F 1 0 0 0 1 1 1 1 0
Taxon Random characters
2 3 6 7 8 11 13 16 18
Outg. 0 0 0 0 0 0 0 0 0
A 0 1 0 0 1 0 0 0 1
B 0 1 0 0 0 0 0 1 0
C 0 1 0 0 1 0 1 1 1
D 1 0 0 0 0 0 1 1 0
E 1 0 1 1 0 1 1 1 1
F 1 0 1 1 0 1 1 1 0
x999, plus original
C
Frequency
Sum of tree lengths
Mean of NND using RF
ILD p-value
= (No. lengths ≤ original) / 1000
= 126 / 1000 = 0.126
IRD p-value
= (No. differences ≥ original) / 1000
= 384 / 1000 = 0.384

Figure 1.

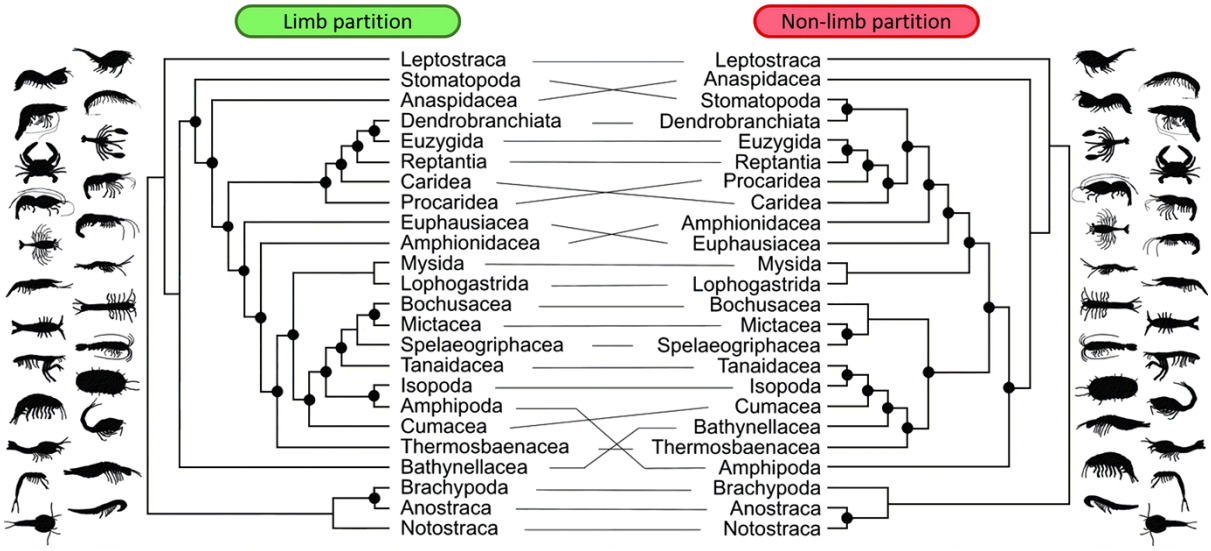
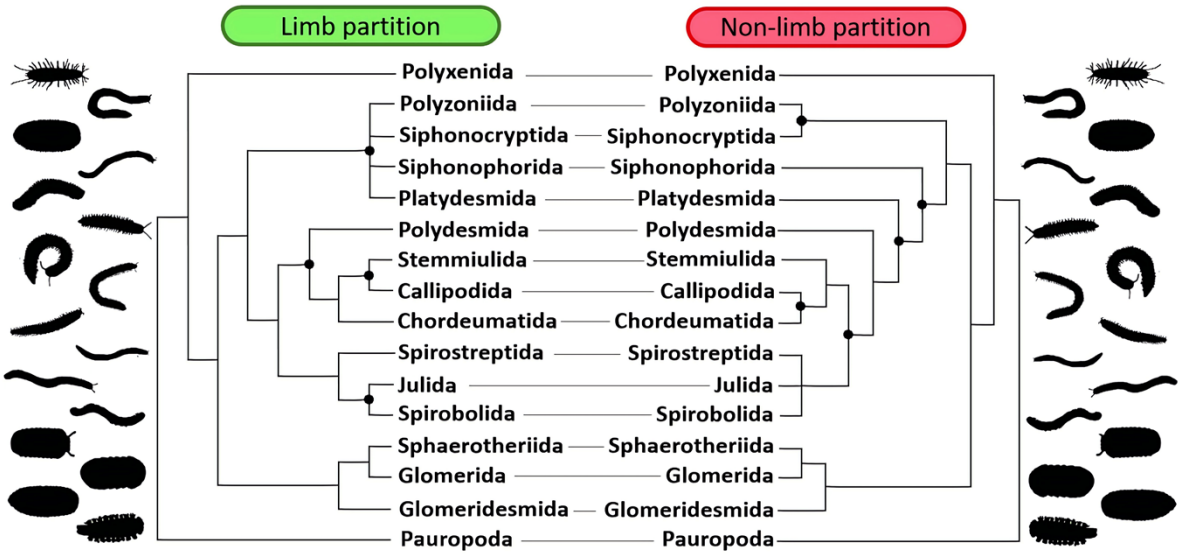

Limb partition
Non-limb partition
Leptostraca
Stomatopoda
Anaspidacea
Dendrobranchiata
Euzygida
Reptantia
Caridea
Procaridea
Euphausiacea
Amphionidacea
Mysida
Lophogastrida
Bochusacea
Mictacea
Spelaeogriphacea
Tanaidacea
Isopoda
Amphipoda
Cumacea
Thermosbaenacea
Bathynellacea
Brachypoda
Anostraca
Notostraca
Leptostraca
Anaspidacea
Stomatopoda
Dendrobranchiata
Euzygida
Reptantia
Procaridea
Caridea
Amphionidacea
Euphausiacea
Mysida
Lophogastrida
Bochusacea
Mictacea
Spelaeogriphacea
Tanaidacea
Isopoda
Cumacea
Bathynellacea
Thermosbaenacea
Amphipoda
Brachypoda
Anostraca
Notostraca

Figure 2.

849



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851

852 **Figure 3.**

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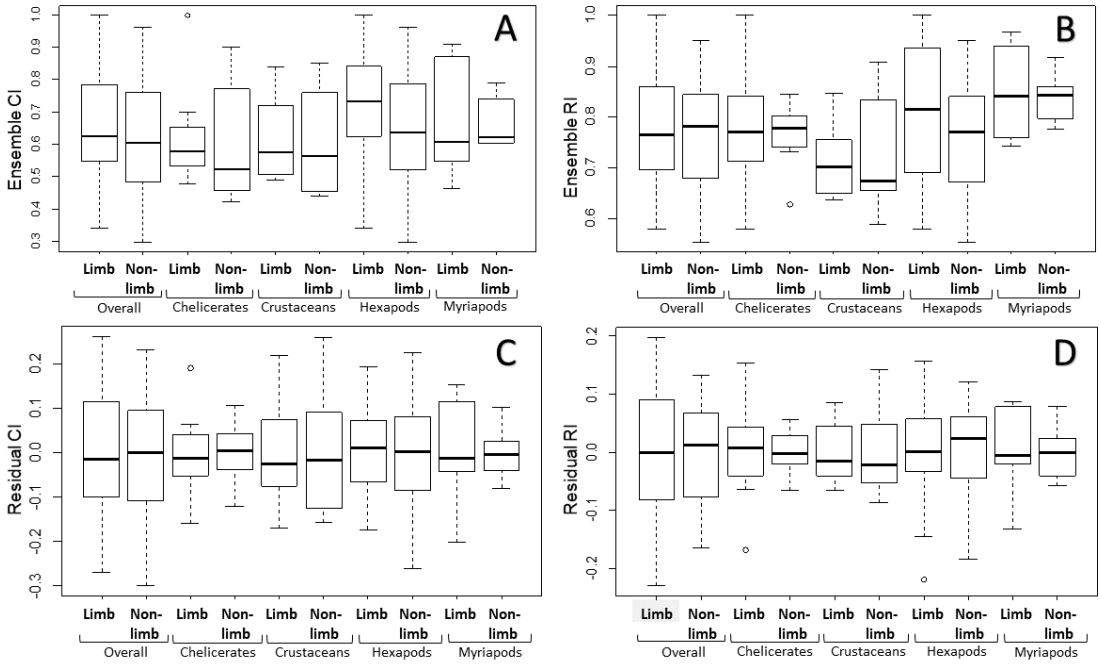

Figure 4

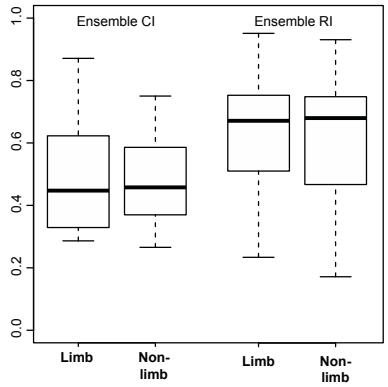

Figure 5